Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE CAUSE OF GYNANDROMORPHISM IN INSECTS

T. H. MORGAN.

In recent years many cases have been recorded in the group of insects in which parts of the body show the characters of the male and other parts those of the female. Most frequently the separation lies along the middle line of the body, so that one side is like the male and the other like the female. About two years ago I attempted in the case of the bee to correlate this result with the well known frequency of dispermy of the insects' egg.[1] Two spermatozoa having entered, one fuses with the egg nucleus and its products produce the female characters; the other develops alone and gives the characters of the male to the parts of the body it supplies with nuclei, etc.

That the latter assumption is not arbitrary is shown by experiments with the egg of the sea-urchin in which it has been possible to fertilize a non-nucleated piece of the egg with a single spermatozoon. Boveri has attempted to prove that under these conditions the characters of the larvae are paternal, which is in accord with our hypothesis for the bee. The evidence however on which Boveri's conclusion rests has been disputed. More recently Godlewski has succeeded in cross-fertilizing a non-nucleated fragment of the egg of a sea-urchin with the sperm of a crinoid. The characters of the young larvae are said to be maternal, indicating that the protoplasm rather than the nucleus is the controlling factor in determining the characters, but Godlewski's statements apply only to the very earliest stages of development, where according to Driesch's results the maternal influences predominate.

A test of the view that I have suggested should be found for the bee if a gynandromorph should arise in a cross between two species; for, on my hypothesis those parts that develop from the combined nuclei should be female and hybrid in character, while those that come from the single nucleus of the spermatozoon should be male and paternal in character. The most remarkable case of gynandromorphism that has ever been described, namely, that of the Eugster hive, resulted from a cross between two species of bees, but it is impossible to tell from von Siebold's description the specific characters of the male and female parts. A test case is apparently furnished in a recent paper by Toyama[1] "On Some Silk-worm Crosses with Special Reference to Mendel's Law of Heredity." Since Toyama has not attempted to draw any conclusion from the interesting cases that he has found I venture to call attention to their possible interpretation.

---

[1] Morgan, T. H. An Alternative Interpretation of the Origin of Gynandromorphous Insects. *Science*, 1905, vol. 21.

A cross was made between two races of silk-worm moths; the female belonged to a European breed having striped caterpillars; the male belonged to the common Japanese breed having plain, *i. e.* not striped, caterpillars. Two of the hybrid caterpillars had the left side of the body striped (maternal) and the right side plain. Applying my hypothesis to this case we see that the striped side is due to the combined nuclei — the striped character carried by the egg dominating the plain character of the sperm-nucleus; the plain side is due to the sperm nucleus alone and is therefore paternal.

It might possibly be objected that the striped race was not pure but produced some plain germ cells, so that the right side is due to this condition; but there is no evidence that the striped race is impure in this respect and the many experiments made by Toyama with this race would have shown the impurity had it existed.[2] Moreover the striped condition of the left side shows that the egg of this individual must have carried striped characters since this character is not carried by the sperm.

Boveri suggested a different interpretation of gynandromorphism. He assumed that the results are due to the single sperm, that enters, fusing with one pole alone of the segmentation spindle derived from the egg nucleus. Toyama's case offers an opportunity to test whether Boveri's or my own hypothesis applies here. For example, according to Boveri's view the single nucleus (that supplies the male parts in the bee) is derived from the egg which in the present case contains the striped character; the other side is derived from the combined nuclei which should also the striped in the present case since this is the dominant; but the facts are contradictory to the hypothesis. On the other hand the facts are what my hypothesis calls for.

---

[1] Toyama, K. Studies on the Hybridology of Insects. I. On Some Silkworm Crosses, with Special Reference to Mendel's Law of Heredity. *Bull. Col. Agric. Tokyo Imperial University*, 1906, vol. 7.

[2] The striped race was found, however, to be impure in another respect. It may produce a pale form but the occurrence of the pale form has no bearing on our conclusion.

So far I have attempted to consider Toyama's cases without regard to the question of the sex of the right and left halves because while this raises some even more interesting issues, the conclusions are more problematical, since we do not know in the moth the nature of the factors that determine sex. Several possibilities must be considered. If however we are justified in extending the conclusion reached above in regard to the origin of these gynandromorph — a conclusion I repeat, that is reached independently of the question of sex — to the case of the bee, where more is known in regard to sex determination, we shall be led to some far reaching and important considerations concerning sex determination.

The moth that emerged from Toyama's gynandromorph caterpillar had on the left striped half of the abdomen, external female reproductive organs; and on the right plain half, male organs. In my view the right side has come from the single spermatozoon. It has produced the male sex. Two interpretations are here possible. If there exist in the silk-worm moth two kinds of spermatozoa — male and female producers — as shown by Stevens and Wilson for some other insects, the right side may be due to a male-producing (arrhenotokous) spermatozoon; while the opposite female side would be due to a female-producing (thelytokous) spermatozoon having fused with the indifferent (?) egg nucleus. On the other hand the results may be due to a single nucleus alone being capable of forming the male characters only. The evidence, even for the egg is not clear for the moths, for while cases have been described in which only females appear from unfertilized eggs, there are other cases in which both males and females developed. Until we know something of the behavior of the polar bodies in these cases it is unsafe to draw any conclusion in regard to the eggs, and much more so in regard to the spermatozoa.

In the case of the bee these conditions are better understood. It appears as a rule that all unfertilized eggs produce males, and all fertilized eggs produce females. The latter result must be due to all the sperm being female producers, or to only female sperm being capable of entering the egg, or to a quantitative relation, namely, the combined nuclei producing female characters and the single nucleus producing male characters. If we are justified in extending to the bee the conclusion reached above for the moth we can decide amongst these three interpretations. If the gynandromorphous bee is due to one sperm nucleus fusing with the egg nucleus and one (or more) sperm nucleus failing to fuse but developing alone, then the sperm are not female-producing but alone are male-producing. The egg nucleus alone is also male-producing as seen in the development of drones. Combined, however, these two male-producing nuclei give rise to a female-producing nucleus. If this conclusion proves to be correct it throws an interesting light on one of the ways in which sex determination is accomplished.

Equally important is the conclusion to which we are led in regard to the relative influence of the spermatozoon versus that of the egg-protoplasm — a question, as we have seen, on which the experimental embryological evidence is still in doubt. The sperm supplied with egg protoplasm gives rise *in the adult* to paternal characters only, even in those cases like the present one in which the egg carries the dominant characters! If we think of the spermatozoon as introducing a nucleus only, the paternal characters may be attributed to the nucleus; if we think of the spermatozoon as introducing also some cytoplasm — the centrosphere for example — the results might be supposed to be due either to the introduced nucleus, or to the introduced cytoplasm, or to both. Since however the egg also supplies cytoplasm (and that of the dominant kind in the present case) this would offset that of the spermatozoon. It seems therefore that the nucleus is the essential factor. Thus our analysis furnishes a clue as to what part of the sperm carries the factors that determine the characters of the adult organism.

COLUMBIA UNIVERSITY, NEW YORK
Sept. 15, 1907